# The Effects of an Ectoparasitic Gastropod, *Caledoniella montrouzieri*, upon Molting and Reproduction of a Stomatopod Crustacean, *Gonodactylus viridis*

BY

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(2 Text figures)

## INTRODUCTION

SEVERAL AUTHORS have reported the occurrence of a snail living upon mantis shrimps, and the morphology and familial affiliation of this unique gastropod, *Caledoniella montrouzieri*, Souverbie, 1869, have been most completely discussed by ROSEWATER (1969). The host stomatopod usually carries two snails, a smaller male on the posterior ventral thorax, and a larger female at the base of or on the anterior surface of the fifth pleopod. The female snail apparently moves on the ventral abdomen of the stomatopod, since egg capsules are attached to the surfaces of the host pleopods. Although THIELE (1929) described a radula, ROSEWATER (op. cit.) found only a muscular proboscis with no radula in three dissections, leaving the nutritional mode of these snails in doubt. However, ROSEWATER (op. cit.) observed that the tips of the thin pleopodal gills of the stomatopods appeared damaged, and suggested that the gastropods may suck body fluids from the host stomatopod. Rosewater found no other evidence of penetration of the host exoskeleton, but mentioned a mucoid deposit at the site of the snail's attachment to the host. These snails occur on several species of gonodactylid stomatopods in different localities, including *Gonodactylus chiragra, G. smithii, G. platysoma, G. falcatus, G. mutatus, G. viridis,* and *Gonodactylolus paulus* in Madagascar, the Comores Islands, Réunion, the Persian Gulf, the Andaman Islands, Thailand, Indonesia, Australia, New Caledonia, and Samoa (ROSEWATER, 1969, 1975; MANNING, 1968, 1969, and personal communication; personal observations).

This paper investigates the effects of *Caledoniella montrouzieri* upon molting rate, growth, and reproduction of *Gonodactylus viridis*. Although *G. viridis* co-occurs with six other species of Gonodactylidae (*G. chiragra, G. smithii, G. falcatus, G. ternatensis, Haptosquilla glyptocercus, Pseudosquilla ciliata*) on a large tide flat at Phuket, Thailand, where the study was conducted, the snail occurred exclusively on *G. viridis*. The term "parasite" will be used in the broad sense of an organism which imposes a negative effect upon its host, without specification of the mechanisms of inflicting the negative effect.

## METHODS

The stomatopods were collected from their coral rubble habitat, measured, their parasitic condition (including ovipositions by the snails) noted, and maintained individually in plastic bowls and aquaria with normal laboratory lighting at the Phuket Marine Biological Center. Field and laboratory temperatures approximated 26°-27° C. The stomatopods were fed crustaceans and mollusks and the water was changed every second or third day. The stomatopods were examined daily for molts and ovipositions. Stomatopods can be successfully maintained, showing normal growth and reproduction, for as long as a year using these methods; the stomatopods were maintained at Phuket about six weeks (see REAKA, 1975, 1976). At the end of the study the stomatopods were killed and preserved in 10% formalin, then changed to 70% ethyl alcohol. The snails remained attached throughout this treatment.

Molting frequencies are too low in stomatopods to establish molting rates for individuals. The most reliable measure of molting frequency in stomatopods is the population molting rate, MR, derived from the total molts in the sample population/total number of stomatopod maintenance days (MR=ΣM/ΣSMD). This index of molting rate provides results consistent with a variety of other field and laboratory methods used independently to assess the frequency of molting in populations, and is least influenced by sample sizes, maintenance time, and the effects of slowly or rapidly molting individuals in the populations. Molting rate does not decline with increased maintenance time (REAKA, 1975). The several species of stomatopods at Phuket, including the parasitized and nonparasitized *Gonodactylus viridis,* were maintained simultaneously for relatively short periods of time under identical conditions. To assess the reliability of the MR, population molting rates were calculated for each of 10, 6, 5, and 4 independently collected subpopulations of four other species (*Gonodactylus zacae, G. falcatus, G. chiragra,* and *Pseudosquilla ciliata*). The sample sizes of these subpopulations approximated those of the parasitized and nonparasitized *G. viridis.* The standard errors (SE) of the MR, calculated from the molting rates of each of these subpopulations were 0.039, 0.030, 0.012, and 0.022 for the 4 species respectively. The subpopulations of *G. zacae, G. falcatus,* and *P. ciliata* were maintained over different seasons and years, although the five subpopulations of *G. chiragra* were maintained simultaneously at Phuket. These results indicate that the MR values presented for the parasitized and nonparasitized *G. viridis,* as well as the other species from Phuket which were maintained simultaneously with *G. chiragra,* probably are reliable within approximately 0.01 or at most 0.04 MR units (see REAKA, 1975, 1978).

Molting growth increments (G/M) were determined by measuring nine linear characters of the exuvium and the hardened postmolt exoskeleton (see REAKA, 1975, 1978), which represented most of the major body dimensions. Growth was determined by the percentage difference between the postmolt and premolt exoskeletons and averaged for all of the nine morphological characters.

Reproductive condition was assessed by the presence of extruded egg batches carried by the females.

## RESULTS

Of the 56 parasitized *Gonodactylus viridis,* four were occupied by a single rather than two *Caledoniella montrouzieri.* The anterior (male) snail was missing in two cases, the posterior (female) snail was lost in one, and the site of loss was undetermined for one individual. These results suggest that were was no differential loss or failure to colonize the anterior or the posterior attachment site on the host stomatopod.

One stomatopod carrying a pair of reproductive snails molted overnight; the snails and their eggs subsequently were found intact on the postmolt host. Unfortunately I was unable to observe the behavioral events which allowed the snails either to remain in place or regain their position while the exuvium was shed. Also, the fate of the eggs deposited prior to the molt was not determined. Presumably they were eaten along with the exuvium by the stomatopod, and the snail deposited new egg cases upon the postmolt stomatopod.

*Caledoniella montrouzieri* occurred on 13.4% of the population of *Gonodactylus viridis.* The snails occurred and reproduced on both sexes of stomatopods over a wide range of sizes. *G. viridis* acquire adult sexual morphology at 15 mm in length, although they continue to molt and grow throughout their life. Snails parasitized only stomatopods ≥ 15 mm in length. Considering all individuals beyond this size, Figure 1 shows that parasitized *G. viridis* were smaller than nonparasitized individuals ($\overline{X}$=29.5, 34.2 mm; $p < 0.001$, $t=3.9$; N=56, 345). If juvenile stomatopods (<15 mm) were also included, the t– test value ($\overline{X}$=29.5, 34.1; $t=1.9$; N=56, 361) fell just below the critical statistic for $p < 0.05$ that parasitized individuals were smaller than nonparasitized stomatopods. Two observations, however, suggested that the juvenile stomatopods did not represent available hosts and should not be included in the samples comparing body size in parasitized

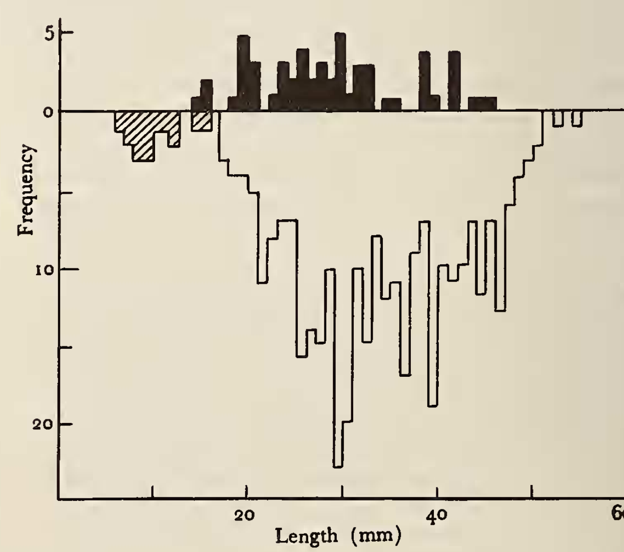


Figure 1

Frequency distribution and body size (total length) of *Gonodactylus viridis* which are not parasitized (open histogram) and parasitized (black histogram) by *Caledoniella montrouzieri.* Hatched histogram indicates juvenile *Gonodactylus viridis* *vs.* nonparasitized *G. viridis*. Although 14.0% (56/401) of mature *G. viridis* were parasitized, none of the 16 juveniles collected were parasitized (0/16 rather than the expected 2.24/16). In addition, although adult snails showed extreme site specificity on the host, small snails showed some irregularity in their site of attachment, suggesting that they initially colonize small but sexually mature stomatopods. Therefore, considering samples of sexually mature hosts, the presence of snails definitely is associated with small size of the host.

These results suggest either that the snails inhibit growth of the host, or that the snails prefer small hosts or are selectively removed from large hosts. The four stomatopods occupied by single rather than both snails ranged from 16-55 mm in body length, and showed no trend for large hosts of either sex to remove or lose parasites more efficiently than small hosts. Therefore, the effects of the snails upon the molting rate of the hosts were examined.

Of 361 nonparasitized individuals, 4.2% molted during the relatively short period of maintenance (10/182 females, 4/163 males, and 1/16) juveniles; of 56 parasitized individuals (35 females, 21 males), only one female (1.8%) molted. The number of stomatopod maintenance days/molt for the nonparasitized population sample was 571 days, while the number of days/molt for the parasitized sample was 1415 days. The molting rates (MR) calculated for the nonparasitized and parasitized subpopulations were 0.18 and 0.07, respectively (SE $\simeq$ 0.01, see above). Figure 2 shows the molting rates calculated for the seven sympatric species of gonodactylids from Phuket. Compared to the

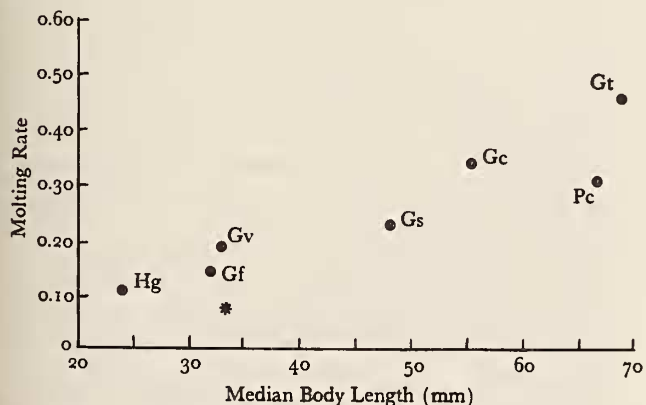


Figure 2

Relationship of molting rate (MR) to body size in 7 populations (closed circles) of nonparasitized stomatopods which were maintained simultaneously in Phuket, Thailand. The closed circle for *Gonodactylus viridis* (Gv) refers to the nonparasitized population sample, and the star refers to the parasitized population sample of *Gonodactylus viridis*. Refer to the text for explanation and reliability measures of MR and for explanation of species.

MR for other species, which increase regularly with body size in this and other stomatopod assemblages (REAKA, 1975, 1978), and to the MR for nonparasitized *Gonodactylus viridis,* parasitized individuals showed significantly depressed molting rates.

Growth increments were available for only three *Gonodactylus viridis* because molting individuals eat their exuvium. The %G/M for the parasitized female was 2.8%, while the two nonparasitized females grew 2.8% and 5.0%, respectively.

Of 182 nonparasitized female *Gonodactylus viridis,* 32 females (17.6%) carried egg batches; of 35 parasitized *G. viridis* females, none were ovigerous (p=0.003, Fisher exact probability test). These results suggest either that females which bear snails do not reproduce, or that snails do not live on or are removed from reproductive female stomatopods.

## DISCUSSION

This study pertains to two questions: (1) the nutritional biology of *Caledoniella montrouzieri,* a gastropod formerly classified as commensal upon its stomatopod host; and (2) the co-evolutionary biology of a sessile organism which lives upon a crustacean host which must molt to grow.

The smaller body size of parasitized than nonparasitized stomatopods suggests that the snail in some way may inhibit growth of the host, although these results also could be obtained by avoidance of or selective removal from large host individuals. No observations suggest that snails selectively avoid large stomatopod hosts. Also, there is no evidence that large stomatopods lose snails more frequently than small hosts, since molting frequencies which might lead to shedding of parasites do not change over ontogeny in stomatopods (REAKA, 1975, 1978), and since single snails are not differentially lost by large host stomatopods. In contrast, several lines of evidence suggest that the presence of snails inhibits growth. Lower percentages of parasitized than nonparasitized individuals molt. Infected stomatopods show longer intermolt intervals and lower molting rates (MR) than noninfected hosts. No effect of the snail upon molting growth increment could be detected, but samples were too small to permit any conclusions.

Failure of parasitized stomatopods to reproduce may result from mechanical obstruction to mating, since the male snail occupies the 7th sternal ridge directly posterior to the ovopore of the stomatopod. The ventral copulatory tubes of the male stomatopod are inserted into the seminal vestibule on the 6th thoracic sternite of the female; copulation may be prerequisite for ovoposition and may be prevented by the presence of the snail. It seems unlikely that snails either avoid reproductive females or that reproductive females are completely effective in removing snails. Considered in combination with the effects of the snail upon molting frequencies, it seems possible that the snails obtain nutrients from the host stomatopod and therefore inhibit reproduction. Regardless of the proximate cause, parasitism by snails imposes complete reproductive failure upon the host stomatopod.

Therefore, *Caledoniella montrouzieri* inflict both decreased growth rates and reproductive failure upon their host. These results support ROSEWATER's (1969) suggestion that the snails, even though lacking a radula, may obtain nutrients by sucking on the thin abdominal gill filaments of the host stomatopod. An alternative and not mutually exclusive hypothesis derives from the disadvantage of host molting for the gastropod, which may lead to selection for the snail to provide some misinformational cue which inhibits molting of the host. The integration of molting in Crustacea is known to be complex and mediated by neuroendocrines (HIGHNAM & HILL, 1969). Although one pair of snails successfully survived and reattached after the molt of the host, four stomatopods carried only one snail, indicating that snails occasionally lose their host; molting of the host seems a logical time for loss to occur. Also, molting of the host probably inflicts considerable loss of reproductive investment upon the snail. Therefore, there may be a selective advantage for the snail to inhibit molting in the host either by neuroendocrinological cues or by depleting the energy supply of the host. Obtaining nutrients may not only decrease the probability of the host molting, but also reaps obvious energetic benefits for the parasite. Therefore, progression from a commensal to a parasitic condition may occur very rapidly in symbionts of arthropods with indeterminant molting and growth.

In addition, molting rates may be instrumental to the extreme specificity of *Caledoniella montrouzieri* on *Gonodactylus viridis* at Phuket, where six other morphologically and behaviorally similar species of gonodactylids occur on the same tide flat. *G. viridis* is a small, abundant species with a low intrinsic molting rate which is further lowered by the presence of the snail. Large species of sympatric stomatopods molt frequently (see Figure 2) which may prevent effective parasitism by the snails. Other small species with low molting rates (*G. falcatus, Haptosquilla glyptocerus*) are less abundant than *G. viridis* at Phuket. Thus, successful parasitism of the snail on other species of stomatopods may not be feasible.

## SUMMARY


1. Pairs of the symbiotic gastropod *Caledoniella montrouzieri* occurred on 13.4% of a population of gonodactylid stomatopods, *Gonodactylus viridis*, in Phuket, Thailand. Individual snails were lost in 4/56 cases, but there was no differential loss of anterior (male) or posterior (female) snails and no differential loss according to size or sex of the host. One pair of snails survived and reattached after their host molted.

2. Sexually mature stomatopods which carried pairs of the gastropod were smaller than sexually mature individuals not carrying snails. Juvenile stomatopods did not bear snails.

3. Lower percentages of stomatopods which carried snails molted than those which did not carry snails, although samples were too small for statistical significance. Molting intervals were longer and molting rates were lower for parasitized than nonparasitized *Gonodactylus viridis;* molting rates for parasitized individuals also were low compared to size-specific molting rates for other sympatric species of gonodactylid stomatopods. The snails inflicted no detectable effect upon growth per molt in the three cases observed.

4. Oviposition of *G. viridis* was completely inhibited by the presence of snails.


## ACKNOWLEDGMENTS


I wish especially to thank Edward Bird, Joseph Rosewater, Raymond Manning, Alan Kohn, Roy Caldwell, and Ralph Smith for their interest and valuable comments. This work was supported by NSF Grant GB-37046.


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